

# ESTABLISHMENT AND PERSISTENCE OF MASS HIERARCHIES IN BROODS OF THE BROWN PELICAN

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**ABSTRACT.**—I investigated the roles of intraclutch variation in egg volume and hatching asynchrony in the establishment of mass hierarchies in broods of the Brown Pelican (*Pelecanus occidentalis*). The second egg averaged 2.6% larger than the first and 1.9% larger than the third. In unmanipulated control broods, first eggs hatched an average of 25 h before second eggs, which hatched 40 h before third eggs. On the day the last egg hatched, first chicks averaged 16% heavier than second chicks and 30% heavier than third chicks. Although chick mass at hatching was strongly correlated with egg volume, differences in mass within broods were almost entirely the result of hatching asynchrony. In broods in which I experimentally reduced hatching intervals, initial nestling mass differences were significantly smaller and strongly correlated with differences in egg volume but not with hatching asynchrony. Intra-brood mass differences remained lower in experimental than control broods throughout the first 2 weeks of the nestling period. Furthermore, mass ranks established at hatching were less likely to persist through this period in experimentally synchronized broods than in asynchronous controls. These results indicate that hatching asynchrony promotes the establishment of a more stable size hierarchy. However, the adaptive significance of nestling size hierarchies in Brown Pelicans remains unresolved. Received 10 June 1999, accepted 5 Dec. 1999.

Nestlings within broods of altricial birds often differ considerably in size at hatching (Stokland and Amundsen 1988, Ohlsson and Smith 1994, Viñuela 1996). These initial size differences might result in competitive asymmetries that influence subsequent nestling growth and survival (Ploger and Mock 1986, Bryant and Tatner 1990, Pinson and Drummond 1993). Establishment of a size-based feeding hierarchy within the brood is often regarded as a parental strategy for coping with unpredictable food supplies (the brood reduction hypothesis; Lack 1947, 1954; see Stoleson and Beissinger 1995 for alternative hypotheses). Parents may create a size hierarchy by beginning incubation before the last egg is laid, thereby inducing the clutch to hatch asynchronously (Clark and Wilson 1981, Stoleson and Beissinger 1995). Hatching asynchrony provides first hatched chicks a head-start by giving them the opportunity to feed and grow before their siblings have hatched (Stokland and Amundsen 1988, Magrath 1992, Viñuela 1996). Because hatchling size often is strongly correlated with egg size (Wil-

liams 1994), parents adopting a brood-reduction strategy also are expected to lay a relatively small final egg to enhance the effect of hatching asynchrony on nestling size disparities (Slagsvold et al. 1984).

In this paper, I characterize nestling mass differences within broods of the Brown Pelican (*Pelecanus occidentalis*), a species purported to practice adaptive brood reduction (Pinson and Drummond 1993; but see Ploger 1997). My main objectives are to (1) assess the relative contributions of hatching asynchrony and intraclutch variation in egg size to the establishment of initial nestling mass hierarchies, and (2) determine if initial mass hierarchies persist through the early nestling period. A basic premise of the brood reduction hypothesis is that stable size hierarchies will not develop in synchronously hatched broods (Lack 1947, 1954). I test this premise by comparing the magnitude and persistence of nestling mass disparities between naturally asynchronous and experimentally synchronized broods.

## METHODS

*Study area and field procedures.*—I studied a ground nesting population of Brown Pelicans on two small (5 ha) islands in the Cape Fear River estuary, southeastern North Carolina. In 1992 I worked in a colony of about 400 breeding pairs on South Pelican Island (33° 56' N, 77° 59' W). In 1993 I worked in a colony of about 200 pairs on Ferry Slip Island (33° 58' N, 77° 57' W). I studied 200 nests in 1992 and 100

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TABLE 1. Frequency of occurrence, estimated duration, and estimated time until hatching completed for six stages of hatching in Brown Pelican eggs.

Hatching stage	<i>n</i>	Frequency (%)	Duration (h)	Time (h) until hatching
(1) No external sign visible, but embryonic vocalizations heard	44	5.0	2	32
(2) Small star-shaped fracture in shell	139	15.8	5	29
(3) Elevated star-shaped fracture	62	7.0	2	25
(4) Hole pipped in egg	531	60.3	20	14
(5) Shell cut widthwise from pipped hole	62	7.0	2	3
(6) Shell cap removed or chick free from shell but with membranes still adhering to it	43	4.9	2	1

nests in 1993. I visited nests once each morning, weather permitting, during the laying period (early to mid-April) to mark eggs and determine the order of laying. On the day an egg was first observed, I measured its length (L) and maximum breadth (B) to the nearest 0.01 cm with a Vernier caliper. I then calculated the volume (V; ml) of each egg according to Hoyt's (1979) equation:  $V = 0.51 \times L \times B^2$ .

When egg laying was completed, I reduced the frequency of visits to 2–4 per week until a few days before the end of the incubation period. At this time I resumed daily visits, weather permitting, to record the time of hatching of each egg. Upon hatching, each chick in a brood was uniquely marked with a colored plastic leg band and weighed to the nearest 0.1 g on a portable electronic scale. All chicks in a brood were weighed on the day the last chick hatched (brood day 0) and again 7 and 14 days later (brood days 7 and 14, respectively). When nestling mass exceeded the 300 g capacity of the electronic scale, I used spring scales with capacities of 500 g, 1 kg, or 2.5 kg to measure mass to the nearest 5, 10, or 50 g, respectively. Measurements of most nestlings had to be terminated after brood day 14 to avoid undue disturbance of the increasingly mobile chicks. My frequent visits prior to this time had no discernable adverse effect on nesting success. In fact, nest survival in the sample reported here was slightly higher than in another sample of nests I visited only 3 times during the same period in 1992 (unpubl. data).

*Quantification of hatching time.*—I quantified the degree of hatching asynchrony between two chicks by calculating the difference in their hatching times. I estimated the time of hatching of each chick to the nearest hour using the method of Stokland and Amundsen (1988) and Viñuela (1996). With this method, the duration of each distinct stage of the hatching process is estimated (Table 1) and the time of hatching of a chick is determined based on the hatching stage in which it was last observed. The duration of each hatching stage was estimated to the nearest hour by multiplying its relative frequency by the total duration of hatching, which I estimated to be 33 h (Shields 1998). The duration of stage 1 may have been underestimated because this stage could be detected only when embryos

vocalized, which they did intermittently. For all other stages there was a visible external indicator; consequently, these stages were less likely to be undetected.

I estimated the time of hatching of each egg as follows. When a hatching stage was observed only on the day before a chick was first seen, I assumed that the observation occurred at the midpoint of that hatching stage (Stokland and Amundsen 1988, Viñuela 1996). Thus, the time until hatching was calculated as half the duration of the observed hatching stage plus the sum of the durations of all subsequent stages. When a hatching stage was observed on each of the two days immediately preceding the first observation of a chick, I assumed that the observation of the shorter of the two stages occurred at the midpoint of that stage. This reduced potential errors in estimated hatching times because the midpoint should be closer to the actual time of observation in the shorter than in the longer of the two observed stages.

*Manipulation of hatching asynchrony.*—I experimentally synchronized hatching in 15 broods in 1992 and 36 broods in 1993 by swapping eggs at the same hatching stage ( $n = 45$  broods) or chicks less than 24 h old ( $n = 6$  broods) among triads of nests. On any given day, the number of nests in which eggs were at the same stage of hatching was limited. Consequently, I made no attempt to match eggs or chicks by size when creating these broods. I also altered hatching patterns in another 36 broods in 1992 by removing the first and second eggs on the days they were laid and replacing them with surrogate eggs. First and second eggs were held at ambient conditions on site until the morning the third egg was laid, at which time they were returned to their original nest (Shields 1998). This treatment was designed to synchronize hatching by delaying the onset of incubation until clutch completion.

The two groups in which I manipulated hatching asynchrony are referred to as experimental broods. Broods in which hatching was unaltered are designated as control broods. I assessed the effect of experimental treatments on hatching asynchrony by comparing mean intervals between hatching of first and last chicks in experimental and control broods using a two-tailed *t*-test. Only broods of three, the modal brood size

at hatching, were included in this study. Because of the failure of some eggs in a clutch to hatch, especially those whose incubation was experimentally delayed (Shields 1998), and incomplete data on some that hatched, only 53 experimental and 90 control broods could be used for analysis.

*Initial nestling mass differences.*—I quantified initial nestling mass disparities in each control brood by calculating the differences in mass among siblings in relation to laying order (first – second, second – third, and first – third) on the day the last chick hatched (brood day 0). To evaluate the influence of egg size on these mass differences, I first tested for within-clutch differences in egg size by comparing the mean volumes of all three eggs. Because eggs within a clutch are not independent sampling units, I used a randomized block design to analyze these data. Clutch was a random blocking factor and laying order a fixed treatment factor in a mixed model two-way ANOVA without replication (Zar 1996). Pairwise comparisons of means were made using the Tukey multiple comparison test. I then used simple linear regression to quantify the relationship between egg volume (independent variable) and nestling mass at hatching (dependent variable). Only data from recently hatched chicks (hatching stage 6, Table 1) were included in this analysis. Next, I estimated the hatching mass of all chicks in control broods using this regression. Finally, I compared observed mass differences between siblings to those calculated from the regression to determine the contribution of egg volume to initial nestling mass differences.

I assumed that any mass disparity between siblings that could not be attributed to a difference in egg volume was due to nestling growth during the hatching period. Therefore, I calculated the effect of hatching asynchrony on the establishment of mass disparities by subtracting the mass differences due to egg volume from the mass differences observed on brood day 0. I compared the mass differences due to hatching asynchrony within broods using a two-tailed paired *t*-test. I further investigated the relationship between hatching asynchrony and growth of first and second chicks by regressing the change in chick mass (mass on brood day 0 – estimated hatching mass) on chick age (h) when measured on brood day 0.

The above methods could not be applied to experimental clutches because most consisted of three eggs of the same laying order obtained from three different nests. Instead, I quantified the extent of nestling mass disparities on brood day 0 by calculating the relative difference in nestling mass, defined as the difference in mass between the largest and smallest chicks and expressed as a percentage of the mean mass of all three chicks in the brood on that day (Bryant 1978). To assess how variation in egg volume contributed to these mass differences, I calculated the relative difference in egg volume as the difference in volume between the eggs from which the largest and smallest chicks on brood day 0 hatched, expressed as a percentage of the mean volume of the clutch (modified from Bryant

1978). Hatching asynchrony was calculated as the difference in hatching times between the largest and smallest chicks on brood day 0. For comparative purposes, I also calculated these variables for control broods. I used correlation analyses to assess the influence of relative difference in egg volume and hatching asynchrony on relative difference in nestling mass. Control and experimental broods were analyzed separately. To evaluate the effect that using eggs from three different clutches to create most experimental nests had on egg size variation, I compared mean relative difference in egg volume between control and experimental broods using a two-tailed *t*-test.

*Maintenance of mass differences.*—Because the size of a nestling relative to its siblings, rather than its absolute size, determined its position in the brood hierarchy (Bryant 1978), I used relative measures to quantify within-brood variation in mass as chicks grew during the first 2 weeks of the nestling period. I evaluated the persistence of intrabrood mass disparities by comparing the magnitudes of relative difference in nestling mass on brood days 0, 7, and 14. Only broods in which all three chicks survived to brood day 14 were used in this analysis. Because measurements obtained on the same brood at three different times are not independent, I used a repeated measures ANOVA to analyze these data. Treatment means were compared using the Tukey multiple comparison test. Control and experimental broods were analyzed separately.

The brood reduction hypothesis predicts that mass differences will be smaller in synchronous broods than in asynchronous ones. I tested this prediction by comparing mean relative difference in nestling mass between experimental and control broods on each of the three brood days using two-tailed *t*-tests. To maintain an overall Type I error rate of 0.05 for these comparisons, I adjusted the significance level of each test to 0.017 using the Bonferroni method (Bart et al. 1998).

Calculations of relative difference in nestling mass on brood days 7 and 14 were based on the difference in mass between the largest and smallest chicks on those days. This variable represented the maximum difference in mass within the brood without taking into account the identities of the largest and smallest chicks. Therefore, it cannot be used to evaluate the stability of mass hierarchies because the largest and smallest chicks in a brood in one week may not be the largest and smallest, respectively, the next week. To measure the stability of mass hierarchies, I ranked each chick in a brood according to its relative mass and then determined whether these mass-ranks remained the same or changed from one week to the next. The proportion of broods in which mass-ranks remained unchanged was used as the measure of stability. According to the brood reduction hypothesis, stable mass hierarchies will develop in asynchronous broods, but not in synchronous broods. I tested this premise by comparing the proportions of control and experimental broods in which mass-ranks did not change between brood days 0 and 7 and between brood days 7 and 14.

I used *G*-tests of independence with Yates' correction for continuity to analyze these data.

Data for both years exhibited similar trends and were pooled for all analyses to increase sample size and statistical power. Statistical tests were performed using NCSS for Windows (version 6.0; Hintze 1996). Results are presented as means  $\pm$  SE.

RESULTS

*Initial mass differences in control broods.*—Eggs generally hatched in the order in which they were laid, with first eggs hatching  $25 \pm 1.4$  h (range 4–52 h) before second eggs, which in turn hatched  $40 \pm 1.4$  h (range 8–85 h) before third eggs ( $n = 90$  clutches). The only exceptions were one nest in which the second laid egg hatched first and three nests in which the first and second laid eggs hatched at the same time. Third laid eggs always hatched last. On the day the third egg hatched, mean masses of chicks from first, second, and third laid eggs were  $104.8 \pm 2.8$  g,  $88.0 \pm 1.4$  g, and  $73.9 \pm 0.7$  g, respectively.

Egg volume varied significantly with respect to laying order ( $F_{2,178} = 13.27$ ,  $P < 0.001$ ). First and third eggs had similar volumes ( $97.5 \pm 0.8$  ml and  $98.2 \pm 0.9$  ml, respectively; Tukey test:  $q = 1.98$ , 178 df,  $P > 0.05$ ), but both were significantly smaller than second eggs ( $100.1 \pm 0.8$  ml; Tukey test: first vs second:  $q = 7.05$ , 178 df,  $P < 0.001$ ; third vs second:  $q = 5.07$ , 178 df,  $P < 0.005$ ). Regression of chick mass at hatching ( $y$ ) on egg volume ( $x$ ) revealed that a difference of 1.0 ml in volume resulted in a 0.8 g difference in hatchling mass ( $y = -3.2 + 0.8x$ ,  $r^2 = 0.93$ ,  $n = 40$ ,  $P < 0.001$ ). Thus, on average, the larger volume of second eggs reduced the initial mass difference between first and second chicks by about 2 g and increased the difference between second and third chicks by 1.5 g (Table 2). Consequently, hatching asynchrony generally accounted for all of the mass difference observed on brood day 0 between first and second chicks and between first and third chicks, and 89% of the difference between second and third chicks. Relative difference in nestling mass on brood day 0 was strongly correlated with the hatching interval between the largest (usually first) and smallest (usually third) chicks ( $r = 0.47$ , 88 df,  $P < 0.001$ ), but not with relative difference in egg volume ( $r = 0.19$ , 88 df,  $P > 0.05$ ).

Mass difference	First and second chicks			Second and third chicks			First and third chicks		
	$\bar{x}$	SE	Range	$\bar{x}$	SE	Range	$\bar{x}$	SE	Range
Observed	16.8	2.1	–21.7 to 88.2	14.0	1.2	–7.4 to 42.8	30.8	2.6	–26.6 to 109.1
Attributed to egg volume	–2.1	0.4	–10.4 to 7.4	1.5	0.4	–9.7 to 11.8	–0.6	0.5	–13.7 to 12.9
Attributed to hatching asynchrony	18.9	2.1	–15.1 to 90.5	12.5	1.1	–6.9 to 40.7	31.4	2.5	–19.9 to 112.1

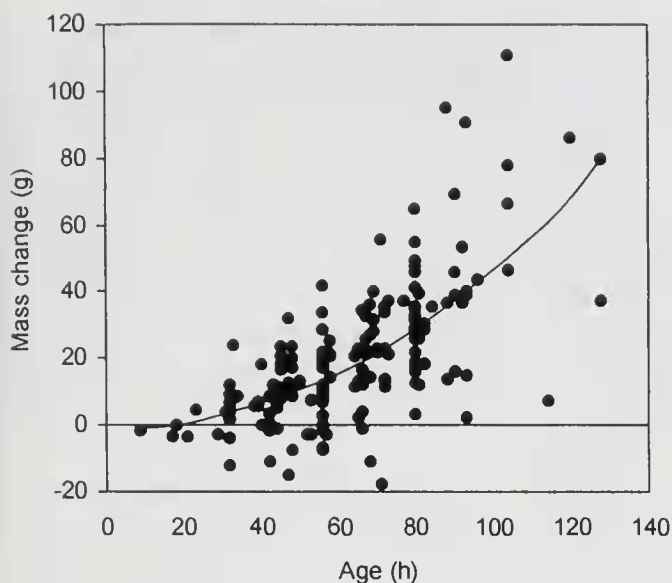


FIG. 1. Relationship between age and change in mass during the hatching period (mass on brood day 0 – estimated hatching mass) for first and second chicks in 90 control broods of the Brown Pelican. Regression equation:  $y = -5.9 + 0.2x + 0.004x^2$ ,  $R^2 = 0.47$ .

Growth of first and second chicks was slow during the first 1–2 days after hatching but increased more rapidly over the next 2–3 days (Fig. 1). Thus, by the time third chicks hatched, first chicks were growing more rapidly than their second siblings. Consequently, mass disparities caused by hatching asynchrony were greater between first and second chicks than between second and third chicks (paired  $t$ -test:  $t = 2.83$ , 89 df,  $P < 0.01$ ; Table 2), even though first-to-second hatching intervals were shorter.

*Initial mass differences in experimental broods.*—Swapping eggs or chicks among some nests and delaying the onset of incubation in others significantly reduced the interval between hatching of first and last chicks in these experimental broods relative to control broods ( $14 \pm 1.6$  h,  $n = 53$  vs  $64 \pm 2.0$  h,  $n = 90$ ;  $t$  with unequal variances =  $-19.60$ , 140 df,  $P < 0.001$ ). Relative difference in nestling mass on brood day 0 was not significantly correlated with hatching asynchrony ( $r = -0.12$ , 51 df,  $P > 0.05$ ). However, it was strongly correlated with relative difference in egg volume ( $r = 0.74$ , 51 df,  $P < 0.001$ ), which was significantly larger in experimental than control clutches ( $7.9 \pm 1.1\%$  vs  $0.6 \pm 0.6\%$ ;  $t$  with unequal variances =  $5.98$ , 87.5 df,  $P < 0.001$ ).

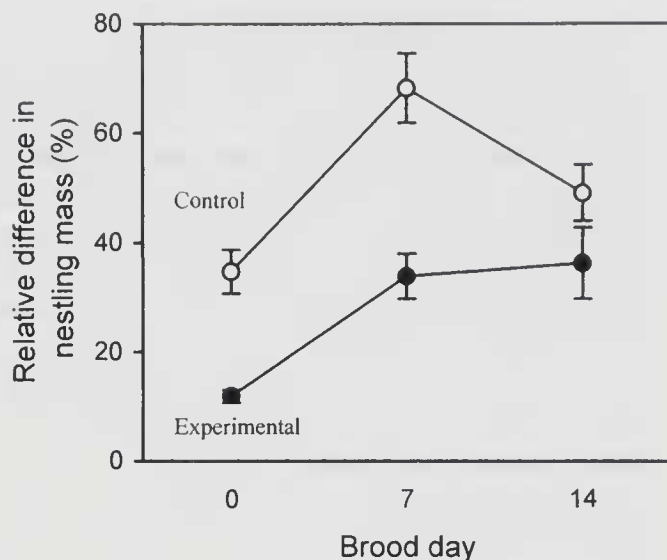


FIG. 2. Relative difference in nestling mass ( $\bar{x} \pm$  SE) for 23 control and 27 experimental broods of the Brown Pelican during the first 2 weeks after hatching.

*Persistence of mass differences.*—Relative difference in nestling mass varied significantly over time in both control ( $F_{2,44} = 41.35$ ,  $P < 0.001$ ) and experimental broods ( $F_{2,52} = 12.90$ ,  $P < 0.001$ ; Fig. 2). Mean relative difference in nestling mass was significantly smaller on brood day 0 than on brood days 7 and 14 in both groups (Tukey test: control: 0 vs 7:  $q = 12.82$ , 44 df,  $P < 0.001$ ; 0 vs 14:  $q = 5.50$ , 44 df,  $P < 0.005$ ; 7 vs 14:  $q = 7.34$ , 44 df,  $P < 0.001$ ; experimental: 0 vs 7:  $q = 5.88$ , 52 df,  $P < 0.001$ ; 0 vs 14:  $q = 6.52$ , 52 df,  $P < 0.001$ ; 7 vs 14:  $q = 0.64$ , 52 df,  $P > 0.05$ ). However, relative difference in nestling mass remained lower in experimental broods throughout the first two weeks of the nestling period (Fig. 2). Differences between the 27 experimental and 23 control broods were highly significant on brood days 0 ( $t$  with unequal variances =  $-5.84$ , 26.3 df,  $P < 0.001$ ) and 7 ( $t = -4.70$ , 48 df,  $P = 0.001$ ), but not on brood day 14 ( $t = -1.50$ , 48 df,  $P > 0.05$ ).

*Stability of hierarchies.*—Mass hierarchies established on brood day 0 were more likely to remain unchanged through brood day 7 in control than experimental broods (19 of 23 vs 8 of 27;  $G = 12.62$ , 1 df,  $P < 0.001$ ). However, mass-ranks on brood day 7 were just as likely to remain unchanged through brood day 14 in experimental as control broods (22 of 27 vs 17 of 23;  $G = 0.09$ , 1 df,  $P > 0.05$ ).

## DISCUSSION

Initial nestling mass disparities within control broods were established primarily by chick growth during the hatching period, which was a function of the degree of hatching asynchrony (Fig. 1). Although hatchling mass was positively correlated with egg volume, the generally larger volume of second eggs lessened the disparity created by hatching asynchrony between first and second chicks by 11% and exaggerated the difference between second and third chicks by a similar amount. Because first and third chicks hatched from eggs of similar size, egg volume had virtually no effect on the large mass differences observed between these chicks (Table 2). In the Shag (*Phalacrocorax aristotelis*), another pelecaniform with similar patterns of egg size variation and hatching asynchrony, initial nestling mass disparities also are almost entirely the result of hatching asynchrony (Stokland and Amundsen 1988). Similarly, egg size variation has a negligible effect on nestling size hierarchies in Blue-eyed Shags (*P. atriceps*; Shaw 1985) and a variety of other asynchronously hatching altricial species in which brood reduction (in the broad sense; Mock 1994) occurs (Magrath 1990, Ohlsson and Smith 1994, Viñuela 1996). Thus, contrary to the suggestion of Slagsvold and coworkers (1984), intraclutch variation in egg size does not appear to be a mechanism by which these brood reducing species facilitate the formation of nestling size hierarchies.

Egg volume had a much stronger influence on initial mass disparities in experimental broods because chicks had little time to grow during the shortened hatching period. This suggests that even in the absence of hatching asynchrony, parents still may be able to produce nestling size hierarchies through intraclutch variation in egg size. However, the importance of egg volume was exaggerated by the experimental procedure. I created most experimental broods using eggs from three different clutches without attempting to maintain the normal degree of intraclutch variation in size. Because egg volume varied more among than within clutches (Shields 1998), this resulted in the mean relative difference in egg volume being an order of magnitude larger in experimental broods than in control broods.

Despite this, initial nestling mass differences within experimental broods were both significantly smaller and less likely to result in the formation of stable mass hierarchies than mass disparities produced by hatching asynchrony in control broods. Therefore, intraclutch egg size variation appears to be unimportant to establishment of stable nestling size hierarchies in either synchronous or asynchronous broods of Brown Pelicans, as was reported for Black Kites (*Milvus migrans*; Viñuela 1996).

Differences in the magnitude and stability of nestling mass disparities between control and experimental broods were due to differences in patterns of nestling growth, which were affected by the degree of hatching asynchrony. Growth of Brown Pelican chicks is slow during the first 24–48 h after hatching, but increases in the following days (Fig. 1), ultimately exhibiting a sigmoidal pattern with an inflection point at about 25 days of age (Schreiber 1976). During the first week after hatching, chicks feed almost exclusively by pecking at partially digested fish regurgitated by their parents onto the floor of the nest (Pinson and Drummond 1993). As chicks grow and become more coordinated in their movements, they begin to intercept regurgitated food from their parents' beaks or pouches before it reaches the nest floor (Pinson and Drummond 1993). Brown Pelican chicks are aggressive throughout the early nestling period, often pecking their siblings both during and between feeding bouts (Ploger 1992, Pinson and Drummond 1993).

Asynchronous hatching in control broods created uneven-aged broods. Older chicks, with their more developed motor skills, were better able to direct their pecks at food and their siblings, giving them an initial advantage in competition for food deposited on the nest floor and in the establishment of dominance-subordinance relationships (Pinson and Drummond 1993). This advantage quickly translated into an even larger size disparity than was present at hatching (Fig. 2). The size advantage afforded first hatched chicks by hatching asynchrony was maintained for at least the first 2 weeks after hatching, and probably persisted until chicks reached maximum mass several weeks before fledging (Schreiber 1976, Pinson and Drummond 1993).

Synchronous hatching in experimental broods, on the other hand, resulted in even-aged broods. The small mass differences resulting from variation in egg volume were insufficient to establish stable mass hierarchies, even though egg volume varied more in experimental than control broods. Instead, differences in motor skills probably were more important initially (Viñuela 1996). Even a slight advantage in coordination of movements may have allowed a chick to establish dominance over its brood mates in the first few days after hatching, regardless of its position in the initial mass hierarchy (Osorno and Drummond 1995). This may explain why mass hierarchies were unstable between brood days 0 and 7, but stabilized during the next week. This also might explain why dominance hierarchies often develop in experimentally synchronized broods of other altricial species (Gibbons 1987, Mock and Ploger 1987, Amundsen and Slagsvold 1991).

According to the brood reduction hypothesis (Lack 1947, 1954), the size hierarchy imposed by hatching asynchrony is a parental evolutionary adaptation for allowing the facultative adjustment of brood size to match the food supply. Should food become too scarce to sustain the entire brood, the smallest chick can be quickly eliminated through sibling competition, thus ensuring partial brood success. Rivalry among the more evenly matched siblings in synchronously hatched broods, on the other hand, would jeopardize survival of the entire brood if food was in short supply (Lack 1947). My findings, while not constituting a test of the brood reduction hypothesis, substantiate several of its basic premises. First, asynchronous hatching, which is controlled mainly by parental incubation behavior (Shields 1998), promoted the development of significantly larger intrabrood mass disparities than synchronous hatching. Second, mass hierarchies established at the completion of hatching in asynchronous broods persisted through at least the first 2 weeks of the nestling period, thus allowing time for brood reduction to occur should food become limited. This period coincides with the time when most mortality of last hatched chicks occurs in this species (Ploger 1992, Pinson and Drummond 1993, Shields 1998). A third key premise of the hypothesis, that stable size hi-

erarchies would not develop in synchronously hatched broods, was not unequivocally supported. Mass hierarchies established at the completion of hatching in the more synchronous experimental broods usually did not remain stable through the first week after hatching. Hierarchies generally stabilized after this time, although mass differences within broods tended to be of lesser magnitude than those in asynchronous broods.

These results suggest that adaptive brood reduction, should it become necessary, could be effected earlier and thereby more efficiently in asynchronous broods than in synchronous broods (Husby 1986, Gibbons 1987, Magrath 1989). However, the potential for unnecessary (maladaptive) deaths of smaller, less competitive siblings also may be higher in asynchronous broods (Clark and Wilson 1981, Stouffer and Power 1990, Pijanowski 1992). Last hatched chicks in Brown Pelican broods often succumb to starvation (Schreiber 1976) or siblicidal attacks (Ploger 1992, Pinson and Drummond 1993). If this mortality represents the adaptive adjustment of brood size when food is scarce, surviving siblings should benefit by receiving the food that would have gone to the third chick had it lived (O'Connor 1978, Stinson 1979), and asynchronous broods should produce more fledglings than synchronous broods (Lack 1947, 1954). Contrary to these predictions, Brown Pelicans deliver less food to their broods after brood reduction than before (Ploger 1997), and asynchronous broods produce fewer fledglings than synchronous broods in poor food years (Shields 1998). These findings, like those of most studies of the adaptive significance of hatching asynchrony (reviewed by Stoleson and Beissinger 1995), do not support the brood reduction hypothesis. Instead, they suggest that mortality of last hatched chicks is a cost, not a benefit, of the size hierarchy imposed by hatching asynchrony in Brown Pelicans. However, size hierarchies may still be adaptive if the reduction in parental effort following brood reduction results in an increase in adult survival and future fecundity (Mock and Forbes 1994). Whether such long-term gains can compensate for the short-term loss of reproduction resulting from brood reduction remains to be determined.

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